

## Nutritional Quality of Leaves and Unripe Fruit Consumed as Famine Foods by the Flying Foxes of Samoa<sup>1</sup>

SUZANNE L. NELSON,<sup>2</sup> MARTIN A. MILLER,<sup>3</sup> EDWARD J. HESKE,<sup>4</sup>  
AND GEORGE C. FAHEY JR.<sup>5</sup>

**ABSTRACT:** Many tropical herbivores alter their diets throughout the year in response to different levels of food availability. Fruit bats, including *Pteropus samoensis* Peale and *Pteropus tonganus* Quoy & Gaimard, are phytophagous species that may increase their consumption of foods such as unripe fruit and leaves in periods of low fruit diversity and volume. These periods include the tropical dry season or following the frequent hurricanes that batter the Samoan Archipelago. We examined the nutritional composition of leaves and immature fruits and compared the levels of organic and mineral nutrients with those of ripe fruit. We used principal components analysis (PCA) to examine patterns of variation in nutrient components of leaves, unripe fruit, and ripe fruit, as well as to compare the mean levels of nutrients. Overall, unripe fruit provided levels of nutrients comparable with those of ripe fruit of the same species for many organic and mineral components. Unripe fruit were only half as rich in iron as ripe fruit, but unripe fruit had high levels of calcium compared with ripe fruit of the same species. Leaves are often cited as a rich source of protein for fruit bats, and our results were consistent with this suggestion. Leaves were also found to be rich in zinc, manganese, and calcium. Therefore, flying foxes and other herbivores probably do not avoid unripe fruits and leaves because of their low nutrient levels. It may be that these famine foods are not normally consumed because of the presence of secondary compounds, low concentrations of palatable sugars, or a distasteful and hard pericarp on unripe fruits.

MANY TROPICAL HERBIVORES alter their diets throughout the year in response to different levels of food availability. For example, the type and volume of food available to the consumer often varies between the wet and

dry seasons in tropical climates. Often, fruit bats consume leaves in greater volume in times of food shortage (Pierson et al. 1996). Leaf consumption, or folivory, is possible through the process of green leaf fractionation, wherein the fruit bat chews the leaf to extract the liquid portion and expels the fibrous residue as a leaf pellet (Marshall 1985, Lowry 1989). This strategy allows monogastric fruit bats that lack the ability to digest fiber to make use of the leaves as a food resource (Lowry 1989) without changes in gut form or function (Kunz and Ingalls 1994). Leaves may be consumed because they provide greater net return per foraging bout than ingestion of large amounts of low-protein fruit or active pursuit of insects (Kunz and Ingalls 1994). Leaves also occur in great volume, are available year-round, and are predictable in time and space (Kunz and Ingalls

<sup>1</sup> Manuscript accepted 18 October 1999.

<sup>2</sup> Biology Department, The University of Illinois, Urbana-Champaign, Illinois 61820. Current address: The Department of Wildlife Ecology and Conservation, University of Florida, Box 110430, Gainesville, Florida 32601 (fax: 352-392-6984; E-mail: snelson@ufl.edu). Author to whom correspondence should be addressed.

<sup>3</sup> Department of Natural Resources and Environmental Sciences, The University of Illinois, Urbana-Champaign, Illinois 61801.

<sup>4</sup> The Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820.

<sup>5</sup> Department of Animal Sciences, The University of Illinois, Urbana-Champaign, Illinois 61801.

1994). Leaves are often consumed by pteropodids throughout the year as a dietary supplement (Tan et al. 1998).

A resource also commonly regarded as a famine food is unripe fruit. Many studies have emphasized that pteropodids prefer ripe over unripe fruit (Foster 1977, Marshall 1985, Banack 1998) and that fruit bats only consume unripe fruit in times of low availability of preferred fruit resources (Funakoshi et al. 1993).

In addition to seasonal fluxes in fruit availability, frugivores must also cope with extreme food stress after severe tropical storms or hurricanes. For example, the flying foxes that inhabit the Samoan Archipelago, *Pteropus samoensis* Peale and *P. tonganus* Quoy & Gaimard, were recently subjected to two violent tropical cyclones. In February 1990, Hurricane Ofa struck Western Samoa with winds in excess of 200 km/hr, and less than 22 months later Hurricane Val struck the same area with the same intensity (Elmqvist et al. 1994, Pierson et al. 1996). Severe and catastrophic storms are typical of the South Pacific region; the Samoan islands are battered with a major storm approximately every 3 yr (Craig and Syron 1992, Craig et al. 1994).

Studies after Hurricane Hugo in the Caribbean demonstrated that some tree species were able to refoliate after 2 weeks and that most species refoliated within 7 weeks (Brokaw and Walker 1991, Frangi and Lugo 1991, Walker 1991, Gannon and Willig 1994), although fruit and flowers took longer. Similarly, in the Samoan Archipelago, many plants stripped of flowers, fruit, and leaves by high winds began to leaf out within days after a storm (Pierson et al. 1996). Leaves, which were more widely available to fruit bats than flowers or fruit in the immediate poststorm period, composed a major part of the poststorm diet, and the majority of feeding observations of *P. samoensis* after both Ofa and Val involved folivory (Pierson et al. 1996). Therefore, switching to folivory after a cyclone may be essential for the success of Samoan flying foxes (Pierson et al. 1996).

Leaves and unripe fruit may be avoided during times when other resources are plen-

tiful because they contain toxic or distasteful secondary compounds, they are structurally difficult to process, they contain a low concentration of sugars, or they do not contain important nutrients. In this study, we examined the nutritional composition of several species of leaves and unripe fruit that could be consumed by fruit bats following seasonal stress or stochastic storm events. We analyzed concentrations of organic and mineral nutrients in unripe fruit and leaves, and compared them with those in ripe fruit of the same species.

## MATERIALS AND METHODS

### *Field Methods*

Samples of leaves and unripe fruit were collected in July of 1996 on Tutuila, American Samoa. Fruits and leaves were collected directly from the tree with a pole or picked while in the tree. Ripe and unripe fruits of five species were selected for comparison. These species were chosen because they were commonly consumed by fruit bats (Banack 1998) and because ripe and unripe fruit could be easily distinguished by the associated color change (Trail 1994). Only fruit pulp was analyzed; the seeds were separated from the pulp and discarded. Similarly, the 10 species of leaves were chosen because of reports in the literature (Marshall 1985, Wilson and Engbring 1992, Banack 1998) or our direct observations that fruit bats consumed them. We collected the samples using latex gloves or using tweezers so that samples would not be contaminated. We were unable to obtain sufficient numbers of new leaves, so we mixed them with approximately equal volumes of mature leaves for analysis. Fruit and leaves were not collected if they showed sign of insect activity. All fruit and leaf samples were placed in plastic bags, labeled, cataloged, and frozen within 8 hr of collection. Specimens of the species collected and cited were compared with the reference collection at the Department of Marine and Wildlife Resources (DMWR) in Pago Pago, American Samoa, and nomenclature follows Whistler (1984).

### Laboratory Analysis

The fruit and leaf samples were analyzed in the Animal Science laboratories at the University of Illinois at Urbana-Champaign. After determination of wet weight, they were dried at 55°C, reweighed, and ground through a stainless steel 2-mm-mesh Wiley mill (AOAC 1975). All samples of the same species were uniformly mixed and a 20-g subsample was removed from the composite sample and used for all analyses thereafter. Nitrogen content of the sample was determined using the macro-Kjeldahl procedure (Bradstreet 1965). Nitrogen values were multiplied by 4.4 to determine the percentage protein within the samples according to Milton and Dintzis (1981). Caloric values were determined using a Bomb calorimeter (Parr no. 1563, Moline, Illinois), and percentage fat was determined using the acid-hydrolysis method (AACC 1983). Samples of each species were dry ashed in a muffle furnace at 500°C for 12 hr to determine ash content, a crude approximation of mineral content. We dissolved the mineral ash in 20% HCl (Fly 1991) and further analyzed the samples using an atomic absorption spectrophotometer (Perkin-Elmer no. 306, Norwalk, Connecticut) to determine concentrations of iron, copper, calcium, manganese, magnesium, zinc, potassium, and sodium. The minerals chosen represent those most often measured for forage studies. Carbohydrate analysis was not attempted because of a lack of laboratory resources. All samples were analyzed in duplicate, and experiments were repeated if the error value between duplicate samples exceeded 5% variability. All concentrations were calculated on a dry-matter basis (DMB). Data for ripe fruit are a subset of a more extensive analysis by Nelson et al. (2000).

### Statistical Analysis

We compared levels of nutrients between ripe and unripe fruit of the same species, and between leaves and ripe fruit. In each analysis, concentrations of nutrients were entered into a principal components analysis (PCA) (Norusis 1993). We used PCA rather than a

discriminate function analysis (DFA) because our analysis was largely exploratory and we had inadequate sample sizes to perform a DFA. We used Hotelling's  $T^2$  test to evaluate differences between ripe and unripe fruit or between leaves and ripe fruit for factor scores generated by the PCAs. Lilliefors's test was used to examine the assumption of normality for each variable, and Levene's test was used to examine assumptions of homogeneity of variances between test groups; all assumptions were met by the factor scores. When a significant difference was detected in the Hotelling's  $T^2$ , univariate  $F$ -tests were used to identify the factor(s) with scores that differed significantly between groups. Separate analyses were conducted on the organic components (nitrogen, dry matter, calories, fat, organic matter) and the mineral components (iron, sodium, calcium, manganese, magnesium, potassium, copper, zinc).

We also used Hotelling's  $T^2$  to test for differences between groups in their mean levels of nutrients. When a significant difference was detected, univariate  $F$ -tests were used to identify the nutrients that differed significantly between test groups. Assumptions of normality and homogeneity of variances were met for comparisons of ripe and unripe fruit. Percentage fat, percentage organic matter, and concentrations of calcium, sodium, and manganese did not meet the assumption of homogeneity of variances for comparisons of leaves and ripe fruit. Because some species had extremely high or low values in each of these categories, transformations of the data did not resolve this problem. We therefore used Kruskal-Wallis tests to compare levels of nutrients between leaves and ripe fruit. All analyses were conducted using SPSS for Windows (Norusis 1993).

## RESULTS

### *Ripe Versus Unripe Fruit*

The PCA based on levels of organic components in samples of five species of ripe and unripe fruit identified two factors (eigen-

TABLE 1  
PCA FACTOR LOADINGS BASED ON LEVELS  
OF ORGANIC NUTRIENTS IN RIPE AND UNRIPE FRUITS  
OF THE SAME SPECIES

PARAMETER	FACTOR 1	FACTOR 2
Eigenvalue	3.05	1.19
Percentage of variation	60.9	23.7
Calories	0.90	0.31
Fat	0.65	0.71
Protein	-0.61	0.70
Organic matter	0.92	-0.33
Dry matter	0.77	-0.01

values  $>1$ ) that together explained 84.7% of the variation (Table 1). Factor 1 loaded heavily and positively for organic matter, calories, and dry matter, and factor 2 loaded heavily and positively for fat and nitrogen. A plot of the factor scores for each sample did not indicate any clear pattern in the variation of organic components that could be used to discriminate between ripe and unripe fruit (Figure 1A). Factor scores did not differ significantly between ripe and unripe fruit (Hotelling's  $T^2 = 0.01$ ,  $df = 2$ ,  $P = 0.97$ ).

Mean levels of organic components in

ripe and unripe fruits were similar (Hotelling's  $T^2 = 0.46$ ,  $df = 5$ ,  $P = 0.85$  [Table 2]). There was no consistent direction of change (increase or decrease) in levels of organic components as individual species of fruit ripened. For example, levels of nitrogen were higher in unripe fruit in three of five species, levels of fat were higher in unripe fruit in one of five species, and caloric content was higher in unripe fruit in three of the five species.

The PCA based on levels of mineral nutrients also identified two factors (eigenvalues  $>1$ ) that together explained 74.6% of the variation (Table 3). Factor 1 loaded heavily and positively for potassium, magnesium, calcium, and manganese, and heavily and negatively for sodium. Factor 2 loaded positively for sodium, manganese, and calcium, and heavily and negatively for iron and copper. Again, a plot of the factor scores for each sample did not show a clear separation of ripe and unripe fruit (Figure 1B), and factor scores were not significantly different between ripe and unripe fruit (Hotelling's  $T^2 = 0.53$ ,  $df = 2$ ,  $P = 0.23$ ).

Mean levels of mineral nutrients did not differ significantly between ripe and unripe fruit (Hotelling's  $T^2 = 4.29$ ,  $df = 8$ ,  $P = 0.79$ ), but individual variation among species also

TABLE 2  
LEVELS<sup>a</sup> OF ORGANIC NUTRIENTS IN RIPE VERSUS UNRIPE FRUITS OF THE SAME SPECIES

SPECIES	% PROTEIN	% FAT	CALORIES	% DRY MATTER	% ORGANIC MATTER
Unripe fruits					
<i>Ficus tinctoria</i>	7.46	8.83	4.34	21.17	90.2
<i>Ficus scabra</i>	11.88	5.93	4.05	12.48	86.7
<i>Planchonella samoensis</i>	8.46	9.28	4.90	32.76	94.1
<i>Terminalia catappa</i>	2.79	3.65	4.42	31.06	95.4
<i>Fagrae berteriana</i>	3.68	12.79	5.36	23.28	96.7
Mean (SD)	6.85 (3.70)	8.10 (3.48)	4.61 (0.52)	24.15 (8.18)	92.62 (4.11)
Ripe fruits <sup>b</sup>					
<i>Ficus tinctoria</i>	6.90	8.96	4.27	17.27	89.6
<i>Ficus scabra</i>	7.59	6.66	4.33	13.68	89.6
<i>Planchonella samoensis</i>	8.64	10.86	4.51	33.75	94.1
<i>Terminalia catappa</i>	3.23	3.11	4.02	17.04	93.5
<i>Fagrae berteriana</i>	3.43	13.20	5.44	28.49	95.5
Mean (SD)	5.96 (2.48)	8.56 (3.88)	4.51 (0.55)	22.05 (8.61)	92.46 (2.71)

<sup>a</sup> Protein is calculated as nitrogen  $\times$  4.4, and calories are reported in kcal/g.

<sup>b</sup> Data for ripe fruits are from Nelson et al. (2000).

TABLE 3  
PCA FACTOR LOADINGS BASED ON LEVELS  
OF MINERAL NUTRIENTS IN RIPE AND UNRIPE FRUITS  
OF THE SAME SPECIES

PARAMETER	FACTOR 1	FACTOR 2
Eigenvalue	4.15	1.82
Percentage of variation	51.9	22.7
Calcium	0.81	0.52
Copper	0.37	-0.57
Iron	0.51	-0.63
Potassium	0.91	-0.30
Magnesium	0.93	0.32
Manganese	0.71	0.52
Sodium	-0.75	0.55
Zinc	0.59	0.24

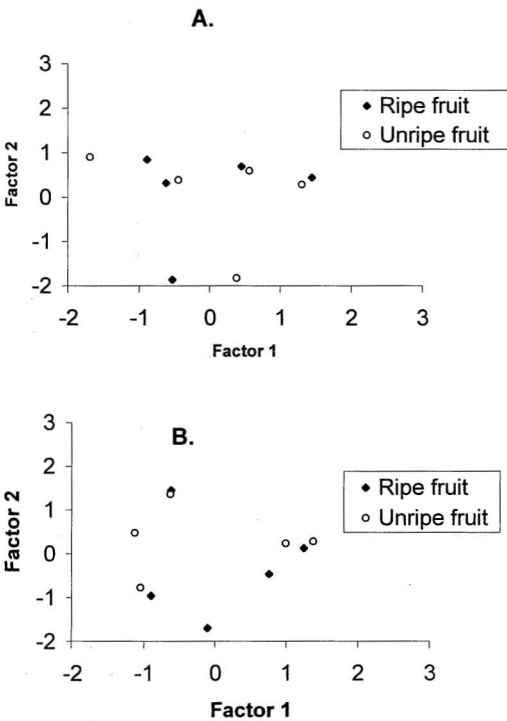


FIGURE 1. Results of the PCA comparing ripe fruit and unripe fruit for factor 1 and factor 2. *A*, Organic components; *B*, minerals.

was high (Table 4). Levels of mineral nutrients often changed dramatically between unripe and ripe fruit of the same species, but there was no consistent pattern among

species in the direction of change as fruit ripened.

#### Leaves Versus Ripe Fruits

The PCA based on levels of organic components in leaves and ripe fruits of 10 species identified two factors (eigenvalues >1) that together explained 72.9% of the variation (Table 5). Factor 1 loaded heavily and positively for calories and organic matter, and heavily and negatively for nitrogen. Factor 2 loaded heavily and positively for fat. A plot of the factor scores for individual samples of leaves and fruit indicated a moderate separation between leaves and ripe fruits (Figure 2). Ripe fruits tended to score somewhat higher than leaves on factor 2, and the two highest scores for factor 1 were from ripe fruits whereas the four lowest scores for factor 1 were from leaves. Factor scores differed significantly between leaves and fruits (Hotelling's  $T^2 = 0.64$ ,  $df = 2$ ,  $P = 0.02$ ). Univariate  $F$ -tests indicated that the means for factor 1 ( $F = 2.67$ ;  $df = 1, 16$ ;  $P = 0.12$ ) were not significantly different, but they were for factor 2 ( $F = 5.26$ ;  $df = 1, 16$ ;  $P = 0.04$ ). Mean levels of nitrogen differed between leaves and ripe fruit ( $X^2 = 4.86$ ,  $df = 1$ ,  $P = 0.03$ ), but mean levels of fat, calories, dry matter, and organic matter did not (all  $P$ -values >0.05 [Table 6]).

The PCA based on levels of mineral nutrients identified three factors (eigenvalues >1) that together explained 67.4% of the variation (Table 7). Factor 1 loaded heavily and positively for magnesium, calcium, and manganese, and negatively for copper. Factor 2 loaded heavily and positively for potassium and copper, and negatively for sodium. Factor 3 loaded positively for sodium and heavily and negatively for iron. Plots of the factor scores for each sample indicated moderate separation of leaves and ripe fruit along factor 1 (Figure 3). Factor scores for leaves and ripe fruit differed significantly (Hotelling's  $T^2 = 1.22$ ,  $df = 3$ ,  $P = 0.004$ ). Univariate  $F$ -tests indicated that factor 1 ( $F = 11.67$ ;  $df = 1, 18$ ;  $P = 0.003$ ) differed significantly between leaves and ripe fruit, but those for factor 2 ( $F = 2.93$ ;  $df = 1, 18$ ;  $P$

TABLE 4  
LEVELS<sup>a</sup> OF MINERAL NUTRIENTS IN RIPE AND UNRIPE FRUITS OF THE SAME SPECIES

SPECIES	CA (mg/g)	NA (μg/g)	K (mg/g)	ZN (μg/g)	MN (μg/g)	MG (mg/g)	FE (μg/g)	CU (μg/g)
Unripe fruits								
<i>Ficus tinctoria</i>	12.28	0.59	37.79	15.00	19.37	5.83	90.97	8.36
<i>Ficus scabra</i>	10.30	1.20	38.02	17.57	4.74	5.29	65.41	9.40
<i>Planchonella samoensis</i>	9.12	1.52	17.00	7.60	19.43	2.32	46.40	4.65
<i>Terminalia catappa</i>	2.24	0.79	28.37	12.85	5.35	2.09	176.90	7.28
<i>Fagrae berteriana</i>	1.06	2.27	11.48	14.29	0.39	2.07	57.37	9.73
Mean (SD)	7.00 (5.0)	1.27 (0.7)	26.53 (12.0)	13.46 (3.7)	9.79 (8.9)	3.52 (1.9)	87.41 (52.6)	7.88 (2.0)
Ripe fruits <sup>b</sup>								
<i>Ficus tinctoria</i>	13.30	0.28	30.16	16.75	12.14	5.84	64.35	7.86
<i>Ficus scabra</i>	12.35	0.70	41.25	20.70	13.41	6.07	102.24	7.03
<i>Planchonella samoensis</i>	9.89	3.37	10.04	13.74	11.24	3.41	14.48	6.36
<i>Terminalia catappa</i>	1.87	1.60	21.40	9.52	0.00	1.91	18.28	7.62
<i>Fagrae berteriana</i>	0.91	2.34	11.26	17.92	1.66	1.82	26.93	4.35
Mean (SD)	7.66 (5.9)	1.66 (1.3)	22.82 (13.2)	15.73 (4.3)	7.69 (6.3)	3.81 (2.1)	45.26 (37.5)	6.64 (1.4)

<sup>a</sup>All calculations are on a dry-matter basis (DMB).

<sup>b</sup>Data on ripe fruits are from Nelson et al. (2000).

TABLE 5  
PCA FACTOR LOADINGS BASED ON LEVELS  
OF ORGANIC NUTRIENTS IN RIPE FRUITS AND LEAVES  
OF THE SAME SPECIES

PARAMETER	FACTOR 1	FACTOR 2
Eigenvalue	2.50	1.15
Percentage of variation	49.9	22.9
Calories	0.90	0.24
Fat	0.28	0.91
Protein	-0.77	0.23
Organic matter	0.91	-0.10
Dry matter	0.44	-0.44

= 0.10) and factor 3 did not ( $F = 0.29$ ;  $df = 1, 18$ ;  $P = 0.60$ ).

Mean levels of calcium ( $X^2 = 10.57$ ,  $df = 1$ ,  $P = 0.001$ ), manganese ( $X^2 = 8.25$ ,  $df = 1$ ,  $P = 0.004$ ), copper ( $X^2 = 5.14$ ,  $df = 1$ ,  $P = 0.02$ ), and magnesium ( $X^2 = 4.01$ ,  $df = 1$ ,  $P = 0.05$ ) differed between leaves and ripe fruit, but levels of sodium, potassium, iron, and zinc did not (all  $P$ -values  $> 0.05$ ). There was no consistent pattern indicating that mean levels of particular nutrients were higher in leaves or fruit, and leaves appeared to be potentially rich sources of some minerals (Table 8). For example, leaves of

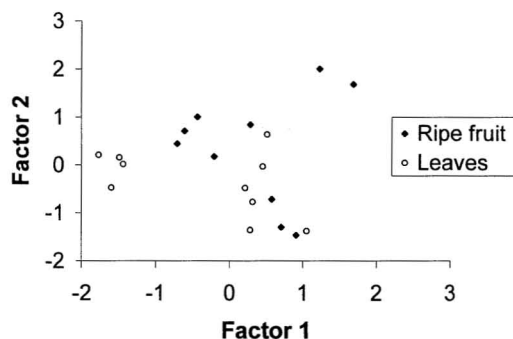


FIGURE 2. Results of the PCA for organic components comparing ripe fruit and leaves for factor 1 and factor 2.

*Ficus unirauniculata* and *Ficus tinctoria* were high in calcium, leaves of *Fagrae berteriana* were very high in sodium, leaves of *Ficus scabra* were high in potassium, and leaves of *Elaeocarpus ulianus* were extremely high in manganese.

#### DISCUSSION AND CONCLUSIONS

In this study, we examined the nutritional composition of leaves and unripe fruit eaten

TABLE 6  
A COMPARISON OF ORGANIC NUTRIENT CONCENTRATIONS<sup>a</sup> FOR LEAVES AND RIPE FRUITS OF 10 SPECIES

SPECIES	% PROTEIN	% FAT	CALORIES	% DRY MATTER	% ORGANIC MATTER
Leaves					
<i>Ficus uniraumicalata</i>	8.99	4.22	3.80	27.05	90.8
<i>Ficus tinctoria</i>	9.58	5.38	3.95	20.94	89.6
<i>Ficus scabra</i>	11.44	4.81	3.88	18.88	89.6
<i>Elaeocarpus ulianus</i>	8.22	4.14	4.60	35.06	96.1
<i>Inocarpus fagifer</i>	9.58	3.47	4.99	32.73	95.7
<i>Callophyllum inophyllum</i>	6.19	4.69	4.85	21.39	94.1
<i>Syzygium inophylloides</i>	4.54	4.22	4.71	44.01	96.2
<i>Fagrae berteroaana</i>	7.75	8.34	4.88	28.09	95.2
<i>Palaquium stehlinii</i>	9.57	5.65	3.95	25.61	97.7
<i>Planchonella samoensis</i>	5.70	3.39	4.49	40.96	95.5
Mean (SD)	8.16 (2.13)	4.83 (1.43)	4.11 (1.75)	29.47 (8.57)	94.05 (2.95)
Ripe fruits					
<i>Ficus uniraumicalata</i>	8.22	5.67	4.22	13.89	80.7
<i>Ficus tinctoria</i>	6.90	8.96	4.27	23.10	82.7
<i>Ficus scabra</i>	7.59	6.66	4.33	13.68	83.2
<i>Elaeocarpus ulianus</i>	4.24	2.29	4.40	23.07	95.5
<i>Inocarpus fagifer</i>	8.07	4.71	4.41	14.93	92.3
<i>Callophyllum inophyllum</i>	3.36	4.19	4.49	25.19	95.2
<i>Syzygium inophylloides</i>	2.00	1.39	4.65	26.76	96.5
<i>Fagrae berteroaana</i>	3.43	13.20	5.44	28.49	94.3
<i>Palaquium stehlinii</i>	4.10	14.29	5.07	24.21	81.9
<i>Planchonella samoensis</i>	8.64	10.86	4.51	33.75	90.9
Mean (SD)	5.66 (2.46)	7.22 (4.45)	4.58 (0.39)	22.71 (6.67)	89.32 (6.4)

<sup>a</sup>Protein is calculated as nitrogen  $\times$  4.4, and calories are reported in kcal/g.

TABLE 7  
PCA FACTOR LOADINGS BASED ON LEVELS  
OF MINERAL NUTRIENTS IN LEAVES AND RIPE FRUITS  
OF THE SAME SPECIES

PARAMETER	FACTOR 1	FACTOR 2	FACTOR 3
Eigenvalue	2.50	1.89	1.00
Percentage of variation	31.2	23.7	12.5
Calcium	0.87	0.04	-0.01
Copper	-0.57	0.57	0.28
Iron	-0.27	0.36	-0.67
Potassium	0.25	0.84	0.04
Magnesium	0.87	0.21	0.11
Manganese	0.59	-0.43	-0.30
Sodium	-0.12	-0.51	0.52
Zinc	0.41	0.49	0.33

by *P. samoensis* and *P. tonganus* in American Samoa. These foods are often consumed during seasonal food shortages or after severe storms and are critical to the consumers be-

cause they are often all that is available to frugivores after these events. We found that both unripe fruit and leaves contained concentrations of many nutrients comparable with those of the ripe fruit preferred by fruit bats in Samoa.

Unripe fruit contained concentrations of organic components that were generally similar to those of ripe fruit. Levels of minerals in unripe fruit were also similar to those in ripe fruit. The most pronounced difference was that concentrations of iron were considerably lower in four of five species of unripe fruit.

Leaves contained higher levels of nitrogen than ripe fruits, indicating higher concentrations of protein, in agreement with Kunz and Diaz (1995). Leaves also tended to have higher levels of calcium, sodium, manganese, and magnesium. Sufficient calcium and sodium levels in the diet are important for fecundity (Batzli 1986, Barclay 1994, 1995) and

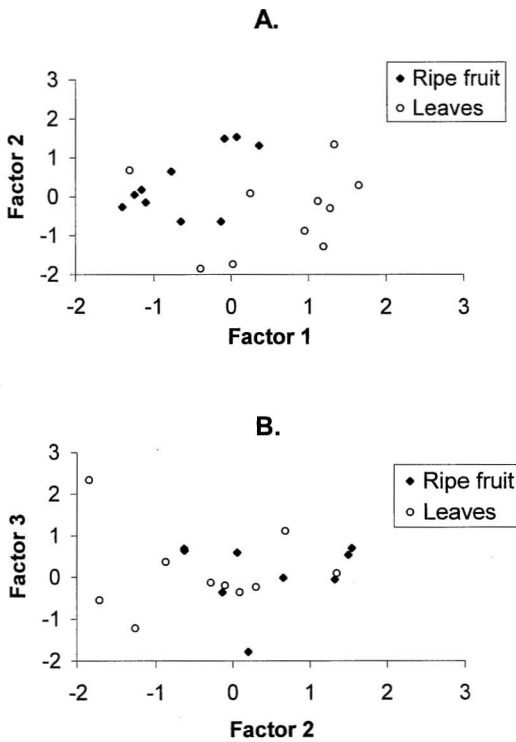


FIGURE 3. Results of the PCA for minerals comparing ripe fruit and leaves. *A*, For factor 1 and factor 2; *B*, for factor 2 and factor 3.

may help to increase bat population numbers after a storm. Thus, famine foods such as leaves and unripe fruit could provide sources of some nutrients, and bats probably avoid consuming these foods during normal foraging for reasons other than their low nutrient levels. In contrast, leaves contained lower levels of fat than ripe fruit in 9 of 10 species. Although we did not analyze leaves or fruit for carbohydrates, we expect that ripe fruits have higher levels of simple sugars. Thus, the energetic value of fruits likely exceeds that of leaves. Our analysis of the caloric value of leaves is probably inflated because it included some indigestible structural plant compounds like cellulose, which the bats expel after chewing. The prediction that leaves do not provide adequate energetic resources should

therefore be further investigated by extracting the indigestible fiber from samples used in future analyses.

Unripe fruit may become a major component of frugivore diets (Yamagiwa et al. 1995) primarily when other food sources are scarce. Bats may generally avoid these foods because they contain high levels of secondary compounds and tannins (e.g., Dasilva 1994). Kinzey and Norconk (1993) found that frugivorous primates continued to consume fruit that contained moderate levels of secondary compounds, but were not attracted to fruit that contained excessive amounts. They also found that frugivores were hesitant to consume fruits that had hard pericarps, which are often characteristic of unripe fruit. Finally, unripe fruits may be passed over by bats because they do not contain adequate levels of sugar to make them palatable (see Baker et al. 1998). Parry-Jones and Auguee (1991) stated that fruit bats in Australia, *Pteropus poliocephalus*, often preferred the same species of fruits that were preferred by humans because of their high sugar content. These variables were not examined in our study, but their influence on food selection by flying foxes deserves further research.

Whatever factors prove to be decisive in determining food selection by flying foxes, it is clear that leaves and unripe fruit contain sufficient concentrations of nutrients to be a potentially important resource. Whether these nutrients can be effectively assimilated should be assessed by metabolic trials. Unripe fruits and leaves may provide a supplemental food source when other more palatable food types are not available.

#### ACKNOWLEDGMENTS

This paper is dedicated to the memory of Marty Miller, an excellent field biologist and a good friend. We thank George Fahey for the use of his laboratory for all analyses. E. Flickinger, M. Wheeler, L. Bauer, D. Hilton, S. Murray, and J. Elizalde provided laboratory assistance. Sincere thanks to J. Aischer, J. Currie, H. Feifeld, A. Brooke, C. Solek, P.



TABLE 8

LEVELS<sup>a</sup> OF MINERAL NUTRIENTS IN LEAVES AND RIPE FRUITS OF 10 SPECIES

SPECIES	CA (mg/g)	NA ( $\mu$ g/g)	K (mg/g)	ZN ( $\mu$ g/g)	MN ( $\mu$ g/g)	MG (mg/g)	FE ( $\mu$ g/g)	CU ( $\mu$ g/g)
Leaves								
<i>Ficus unirauniculata</i>	33.77	1.36	16.32	18.63	40.09	7.68	95.03	6.83
<i>Ficus tinctoria</i>	28.22	0.62	18.89	13.80	19.16	5.76	53.92	4.45
<i>Ficus scabra</i>	27.08	0.85	36.18	17.07	21.19	7.69	89.00	7.68
<i>Elaeocarpus ulianus</i>	18.76	2.24	10.05	13.24	108.31	4.92	72.23	5.58
<i>Inocarpus fagifer</i>	14.13	1.64	18.21	26.76	57.71	4.89	57.71	2.80
<i>Callophyllum inophyllum</i>	6.81	1.61	15.91	11.72	0.93	2.65	39.75	13.98
<i>Syzygium inophylloides</i>	9.57	1.56	3.34	4.65	56.82	3.54	12.48	5.28
<i>Fagrae berteriana</i>	10.43	20.69	5.24	13.49	24.72	3.71	46.97	6.92
<i>Palaquium stehlinii</i>	27.97	0.97	22.45	11.98	13.72	2.51	70.90	6.21
<i>Planchonella samoensis</i>	20.12	1.15	2.97	12.29	17.45	7.24	14.28	4.83
Mean (SD)	6.44 (10.9)	3.27 (6.1)	14.96 (10.2)	14.36 (5.7)	36.01 (34.8)	5.06 (1.9)	55.27 (28.1)	6.46 (2.9)
Ripe fruits <sup>b</sup>								
<i>Ficus unirauniculata</i>	7.41	0.49	20.74	32.00	15.51	4.15	118.69	9.97
<i>Ficus tinctoria</i>	12.28	0.59	37.79	15.00	19.37	5.83	90.97	8.36
<i>Ficus scabra</i>	10.30	1.10	38.02	17.57	4.74	5.29	65.41	9.40
<i>Elaeocarpus ulianus</i>	2.57	0.41	14.95	7.20	10.40	2.30	70.05	8.53
<i>Inocarpus fagifer</i>	3.22	0.23	18.77	15.83	15.83	3.48	95.89	9.20
<i>Callophyllum inophyllum</i>	5.02	1.89	10.24	12.23	0.52	2.51	4.58	6.16
<i>Syzygium inophylloides</i>	2.13	1.92	6.11	7.14	8.44	2.20	221.86	7.04
<i>Fagrae berteriana</i>	1.06	2.27	11.48	14.19	0.39	2.07	57.37	19.73
<i>Palaquium stehlinii</i>	3.27	2.19	18.96	7.51	12.92	2.32	194.99	7.33
<i>Planchonella samoensis</i>	9.12	3.48	12.34	13.32	11.94	3.74	19.73	5.69
Mean (SD)	5.64 (3.9)	1.46 (1.1)	18.94 (10.9)	14.20 (7.3)	10.00 (6.5)	3.39 (1.4)	93.95 (69.5)	9.14 (3.9)

<sup>a</sup> All calculations are on a dry-matter basis (DMB).<sup>b</sup> Data on ripe fruits are from Nelson et al. (2000).

Tuanua, and A. Tualaulelei for their help in finding field sites, identifying fruit and leaf species, and collecting samples.

#### LITERATURE CITED

- AACC. 1983. Approved methods, 8th ed. American Association of Cereal Chemists, St. Paul, Minnesota.
- AOAC (ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS). 1975. Official methods of analysis, 12th ed. Washington, D.C.
- BAKER, H. G., I. BAKER, and S. A. HODGES. 1998. Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica* 30: 559–586.
- BANACK, S. A. 1998. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology* 79: 1949–1967.
- BARCLAY, R. M. R. 1994. Constraints on reproduction by flying vertebrates: Energy and calcium. *Am. Nat.* 144: 1021–1031.
- . 1995. Does energy or calcium availability constrain reproduction by bats? *Symp. Zool. Soc. Lond.* 67: 245–258.
- BATZLI, G. O. 1986. Nutritional ecology of the California vole: Effects of food quality on reproduction. *Ecology* 67: 406–412.
- BRADSTREET, L. S. 1965. The Kjeldahl method for organic nitrogen. Academic Press, New York.
- BROKAW, N. V. L., and L. R. WALKER. 1991. Summary of the effects of Caribbean hurricanes on vegetation. *Biotropica* 23: 442–447.
- CRAIG, P., and W. SYRON. 1992. Fruit bats in American Samoa: Their status and future. Pages 145–149 in D. E. Wilson and G. L. Graham, eds. Pacific island flying foxes: Proceedings of an International Conservation Conference. U.S. Fish Wildl. Serv. Biol. Rep. 90 (23).
- CRAIG, P., P. TRAIL, and T. E. MORRELL. 1994. The decline of fruit bats in American Samoa due to hurricanes and over-hunting. *Biol. Conserv.* 69: 261–266.
- DASILVA, G. L. 1994. Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *Int. J. Primatol.* 15: 655–678.
- ELMQVIST, T., W. E. RAINEY, E. D. PIERSON, and P. A. COX. 1994. Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain forest. *Biotropica* 26: 384–391.
- FLY, A. 1991. Iron bioavailability from diets containing intact fiber sources. Ph.D. diss., The University of Illinois at Urbana-Champaign.
- FOSTER, M. S. 1977. Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology* 58: 73–85.
- FRANGI, J. L., and A. E. LUGO. 1991. Hurricane damage to a flood plain forest in the Luquillo mountains in Puerto Rico. *Biotropica* 23: 324–335.
- FUNAKOSHI, K., H. WATANABE, and T. KUNISAKI. 1993. Feeding ecology of the Northern Ryukyu fruit bat, *Pteropus dasymallus dasymallus*, in a warm-temperate region. *J. Zool. (Lond.)* 230: 221–230.
- GANNON, M. R., and M. R. WILLIG. 1994. The effects of Hurricane Hugo on bats of the Luquillo Experimental Forest of Puerto Rico. *Biotropica* 26: 320–331.
- KINZEY, W. G., and M. A. NORCONK. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *Int. J. Primatol.* 14: 207–226.
- KUNZ, T. H., and C. A. DIAZ. 1995. Folivory in fruit eating bats, with new evidence from *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). *Biotropica* 27: 234–238.
- KUNZ, T. H., and K. A. INGALLS. 1994. Folivory in bats: An adaptation derived from frugivory. *Funct. Ecol.* 8: 665–668.
- LOWRY, J. B. 1989. Green-leaf fractionation by fruit bats: Is this feeding strategy a unique nutritional strategy for herbivores? *Aust. Wildl. Res.* 16: 203–206.
- MARSHALL, A. G. 1985. Old world phytophagous bats (Megachiroptera) and their food plants: A survey. *Zool. J. Linn. Soc.* 83: 351–369.
- MILTON, K., and F. R. DINTZIS. 1981. Nitrogen-to-protein conversion factors for tropical plant samples. *Biotropica* 13: 177–181.

- NELSON, S. L., M. A. MILLER, E. J. HESKE, and G. C. FAHEY JR. 2000. Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. *Ecography* 23:393–401.
- NORUSIS, M. J. 1993. SPSS for Windows. Professional Statistics, Release 6.0. SPSS, Chicago.
- PARRY-JONES, K., and M. L. AUGEE. 1991. Food selection by grey-headed flying foxes (*Pteropus poliocephalus*) occupying a summer colony site near Gosford, New South Wales. *Aust. Wildl. Res.* 18:111–124.
- PIERSON, E. D., T. ELMQVIST, W. E. RAINEY, and P. A. COX. 1996. Effects of tropical cyclonic storms on flying fox populations on the South Pacific islands of Samoa. *Conserv. Biol.* 10:438–451.
- STUDIER, E. H., D. P. VIELE, and S. H. SEVICK. 1991. Nutritional implications for nitrogen and mineral budgets from analysis of guano of the big brown bat, *Eptesicus fuscus* (Chiroptera, Vespertilionidae). *Comp. Biochem. Physiol. A* 100:1035–1039.
- TAN, K. H., A. ZUBAID, and T. H. KUNZ. 1998. Food habits of *Cynopterus brachyotis* (Müller) (Chiroptera: Pteropodidae) in peninsular Malaysia. *Trop. Ecol.* 14:299–307.
- TRAIL, P. 1994. The phenology of rainforest plants in Tutuila, American Samoa. Department of Marine and Wildlife Resources, American Samoa.
- WALKER, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23:379–385.
- WHISTLER, W. A. 1984. Annotated list of Samoan plant names. *Econ. Bot.* 38:464–489.
- WILSON, D. E., and J. ENGBRING. 1992. The flying foxes *Pteropus samoensis* and *Pteropus tonganus*: Status in Fiji and Samoa. Pages 74–101 in D. E. Wilson and G. L. Graham, eds. Pacific island flying foxes: Proceedings of an International Conservation Conference. U.S. Fish Wildl. Serv. Biol. Rep. 90 (23).
- YAMAGIWA, J., T. YUMOTO, and T. MARUHASHI. 1995. Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates* 35:1–14.